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OROBANCHE ARIZONICA SP. NOV. AND NOMENCLATURAL CHANGES IN *OROBANCHE COOPERI* (OROBANCHACEAE)

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ABSTRACT

The taxonomy of plants that have been identified as *Orobanche cooperi, O. multicaulis,* and *O. dugesii* is reassessed, resulting in recognition of three species: (1) *O. cooperi* A. Gray with three subspecies: subsp. *cooperi,* **Orobanche cooperi** subsp. **palmeri** (Munz) L.T. Collins **comb. et stat. nov.**, and **Orobanche cooperi** subsp. **latiloba** (Munz) L.T. Collins **comb. et stat. nov.** (2) **Orobanche arizonica** L.T. Collins, **sp. nov.** (a segregate from *O. cooperi*), and (3) *O. dugesii* (S. Wats.) Munz, retained with no change in status. *Orobanche multicaulis* is a heterotypic synonym of *O. cooperi* var. *latiloba.*

The genus *Orobanche* traditionally has been divided into four sections, sect. *Orobanche* and sect. *Trionychon* Wallr. in the eastern hemisphere, and sect. *Nothaphyllon* (A. Gray) Heckard (*Myzorrhiza* Phil.) and sect. *Gymnocaulis* Nutt. in the western hemisphere. The four sections are recognized based primarily on floral morphology and to a lesser extent by inflorescence architecture. Some recent authors (Schneeweiss et al. 2004a, b) have preferred to divide the genus into five genera, based on molecular phylogenetic data (in which case, the taxa of sect. *Nothaphyllon* are transferred to *Aphyllon* Mitch.), although, some authors, such as Wicke et al. (2013), have put these taxa in *Myzorrhiza* Phil. in error. However, because the genus in the broad sense appears to be a monophyletic lineage and because combinations in the segregates are lacking for many of the North American taxa, we have continued to treat *Orobanche* broadly in the present research toward a forthcoming account in the *Flora of North America* series.

The North American species of sect. *Nothaphyllon* have been divided informally into two groups referred to as the *Orobanche ludoviciana* Nutt. complex (Collins 1973) and the *O. californica* Cham. & Schltdl. complex (Heckard 1973). Species in the *O. californica* complex have inflorescences that are mostly corymbose, whereas species in the *O. ludoviciana* complex have inflorescences that are elongate and racemose. Within each complex, species may be separated by details of floral morphology, ecology, geographic distribution, and host preference.

The present research builds from that of Collins (1973), which has already resulted in the naming of one new species in the *Orobanche ludoviciana* complex (Collins et al. 2009). While preparing the treatment for the Flora of North America, it became apparent that there were taxonomic issues associated with a cluster of taxa within the *O. ludoviciana* complex closely associated with *O. cooperi* (A. Gray) A. Heller. The similarity of these taxa has made determination of species difficult. Munz's (1930) treatment of this group has proven unsatisfactory for determining species in the *O.*

ludoviciana complex. Collins et al (2009) clarified some of the issues regarding this complex of species, however others remain unresolved. This paper addresses *O. cooperi* and closely allied taxa.

Three binomials are the focus of this paper: *Orobanche cooperi*, *O. multicaulis* Brandeg., and *O. dugesii* (S. Wats.) Munz. Three questions are posed: 1) Is there an undescribed species submerged within this aggregation of taxa? 2) Do these three binomials represent three different species? 3) What is the taxonomic relationship between *O. cooperi* and *O. multicaulis*?

A new species of *Orobanche*

During the process of reassessing the taxonomic status of *Orobanche cooperi*, a set of specimens accumulated that were morphologically and ecologically distinct from the plants now determined as that species. They represent populations of a smaller-flowered *Orobanche* with acute corolla lobes found mostly north of the Mogollon Rim and widely distributed in the four corners region of Arizona, New Mexico, Utah, and Colorado (Figs. 1, 2). Previously, these specimens have been identified as either *O. cooperi* or *O. ludoviciana* or sometimes as *O. multiflora*. Three factors initially brought our attention to these plants. They flower in the summer, whereas *O. cooperi* flowers from late winter to late spring. They occur at higher elevations and latitude than populations of *O. cooperi* from the Sonoran Desert. Finally, they utilize *Gutierrezia* as primary hosts, as contrasted with *O. cooperi*, which utilizes mostly *Ambrosia*. The habitat for these plants is either pinyon-juniper woodland or cold desert-shrub associations of the Colorado Plateau and contiguous areas.

Extensive study of the morphology, ecology, and geographic distribution of these populations reveals that they do not fit into the protologue of *Orobanche cooperi* or other *Orobanche* taxa. The principal characters that set these plants apart from *O. cooperi* are as follows: (1) the corollas are shorter (15–20 vs. 16–32 mm); (2) the narrowly acute corolla lobes lack an apiculate tooth (Fig. 3); (3) glands are absent from the anthers (Fig. 4); (4) they flower in mid-summer (June–August vs. January–May); (5) the host plants are *Gutierrezia* (Asteraceae: Astereae) (vs. mostly *Ambrosia*; Asteraceae: Heliantheae) (Table 1); and (6) their distribution is mostly north of the Mogollon Rim (above 1500 m), whereas *O. cooperi* is south of the Mogollon Rim and at lower elevations (Fig. 5). Ecologically these aberrant plants are found in the red sands of the high deserts and pinyon-juniper woodlands of the Colorado Plateau. The larger-flowered *O. cooperi* has not been reported above 1000 m. Collins (1973) noted these factors but did not suggest a nomenclatural solution. R.H. Peebles, who collected the type specimen of this segregate taxon, recognized as early as 1935 that it was different from *O. cooperi*. He annotated the holotype with a note suggesting that the specimen was not typical of *O. cooperi* but might be of hybrid origin. The new segregate is formally described as *O. arizonica* later in this paper.

Reexamining *Orobanche dugesii*

In a limited study for a regional flora in Mexico, Rzedowski (1998), following Collins (1973), indicated that *Orobanche multicaulis* should be reduced to synonymy under *O. dugesii*, based on nomenclatural priority. The question posed here is whether *O. multicaulis* and *O. dugesii* are in fact conspecific. More specifically, the question addresses the relationship between *O. dugesii* and *O. multicaulis* var. *palmeri* Munz, as these two are geographically contiguous (Fig. 5) and some confusion exists as to their circumscription. Apparently, her study included the type specimens of *O. dugesii* and *O. multicaulis* var. *palmeri* but did not include the types for *O. multicaulis* var. *multicaulis* or *O. cooperi* (see discussion below). Although Collins (1973) suggested that the two taxa are conspecific, reducing *O. dugesii* to a subspecies of *O. multicaulis*, his combination was never formally published and are questioned herein. This has led to ambiguity as to the taxonomic status of the two binomials and the associated nomenclature.

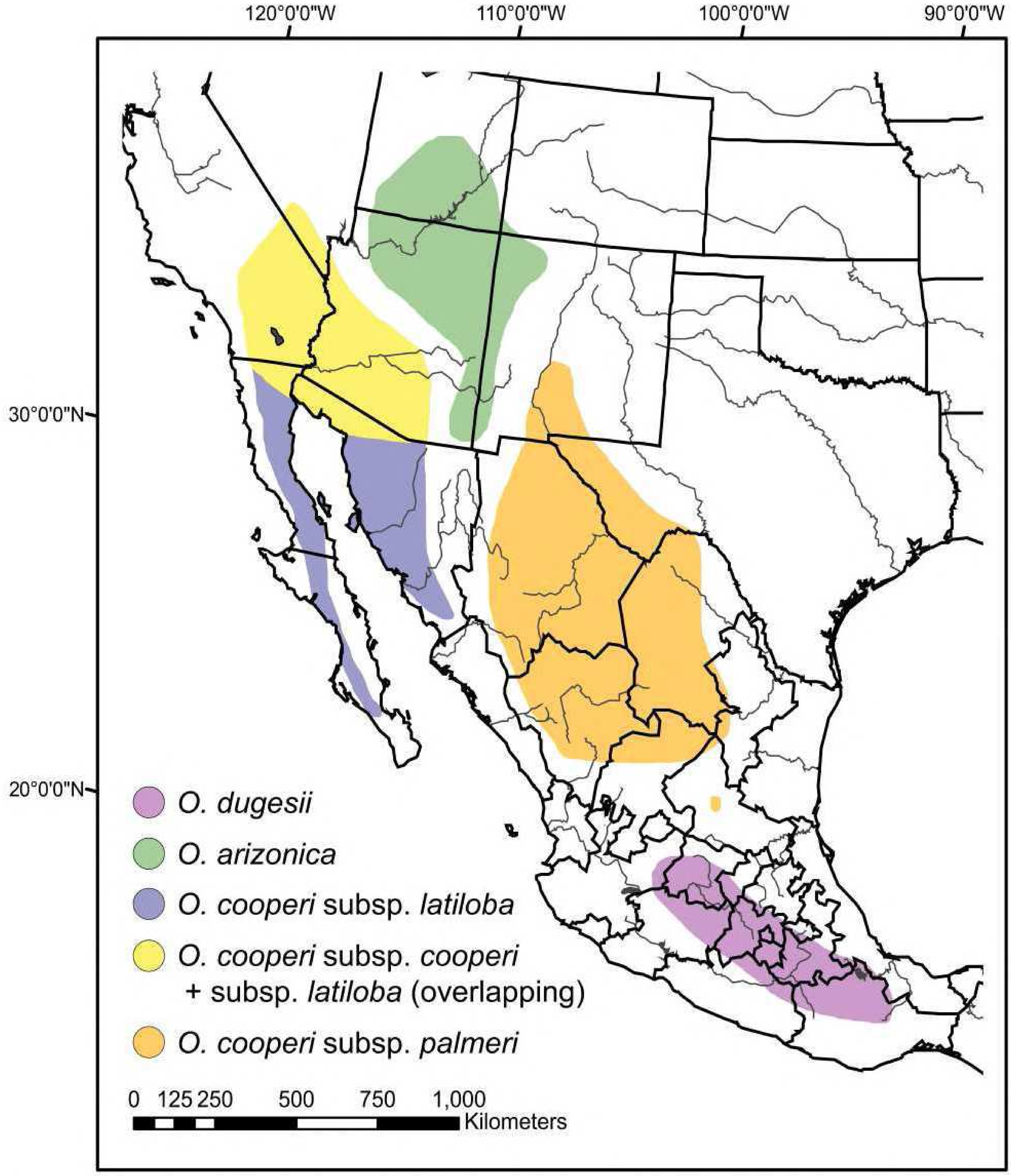

Figure 1. Distribution of taxa in the *Orobanche cooperi* complex, based on representative herbarium specimens examined in the present study.

Figure 2. Habit photograph of *Orobanche arizonica*. Voucher: *Collins 1538* (UWM), collected in San Juan County, Utah. Photo: L. T. Collins.

Figure 3. Habit photograph of *Orobanche cooperi* subsp. *latiloba*. Voucher: *Yatskievych 81-118* (ARIZ, MO), collected in La Paz County, Arizona. Photo: G. Yatskievych.

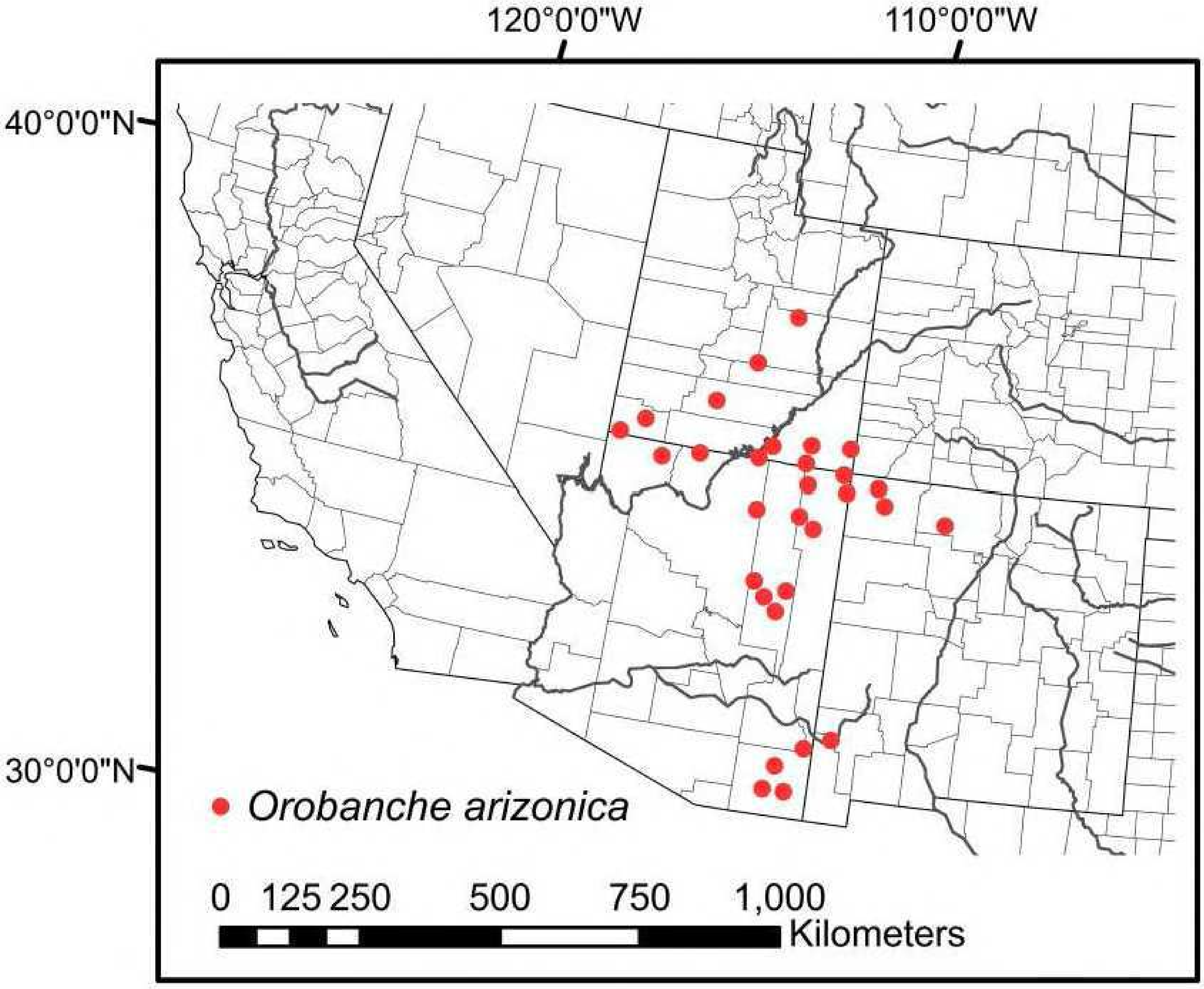

Figure 4. Distribution of *Orobanche arizonica*, based on representative herbarium specimens examined in the present study.

For the present study, a detailed comparison was done of the type specimens for all taxa under consideration, as well as a broader comparison of herbarium material throughout the known ranges of the taxa. We examined 30 herbarium sheets for *Orobanche multicaulis* var. *palmeri*, but only seven sheets for *O. dugesii*. Based on the morphology of the types of *O. dugesii* and *O. multicaulis*, they are indeed distinct taxa (Table 2). *Orobanche dugesii* presents as a much smaller plant (Fig. 6) and lacks the dark purple coloring of *O. multicaulis*. The holotype of *O. dugesii* is essentially glabrous, which is unusual in the group, (a fact noted by Munz [1930]), whereas the holotype of *O. multicaulis* is densely glandular-pubescent (also noted by Munz), which is typical of most *Orobanche* species. The anthers of *Orobanche multicaulis* are usually pubescent and have stalked glands on the dorsal surface (Fig. 3B), characters that are absent from *O. dugesii*. Rzedowski (1998) attributed both conditions of the anthers to *O. dugesii*. Additionally, the palatal folds of *O. dugesii* are glabrous, but those of *O. multicaulis* are densely pubescent. These characters appear to be of critical value in distinguishing the two taxa morphologically. The corollas of *O. dugesii* are short with obtuse or truncate lobes, sometimes bearing a minute apiculate tooth, and are mostly glabrous. Comparatively, specimens assigned to *O. multicaulis var. palmeri* have longer corollas with a more pronounced apical tooth on the lobes and copious indument. The relative paucity of specimens makes it impossible at this time to establish the geographic distribution of *O. dugesii* accurately in relation to *O. multicaulis* var. *palmeri*. However, the two appear to be allopatric in Mexico (Fig. 5). Host data for *O. dugesii* are not available (or questionable, e.g., grass) for most specimens examined, thus preventing any comparison of this aspect of the ecology of the two taxa. Therefore, the plants heretofore identified as *O. multicaulis* var. *palmeri* are recognized as a taxonomic entity distinct from *O. dugesii*. Accordingly, *O. dugesii* is retained as a separate species distributed principally in the Central Mexican Trans-Volcanic Belt (Clausen 1959). *Orobanche multicaulis* is treated further in the following section.

Figure 5. Dissected corolla of *Orobanche arizonica*, taken from *Holmgren & Holmgren 7066* (NY); note the acute, but not apiculate lobes that are ciliate and pubescent with nonglandular trichomes.

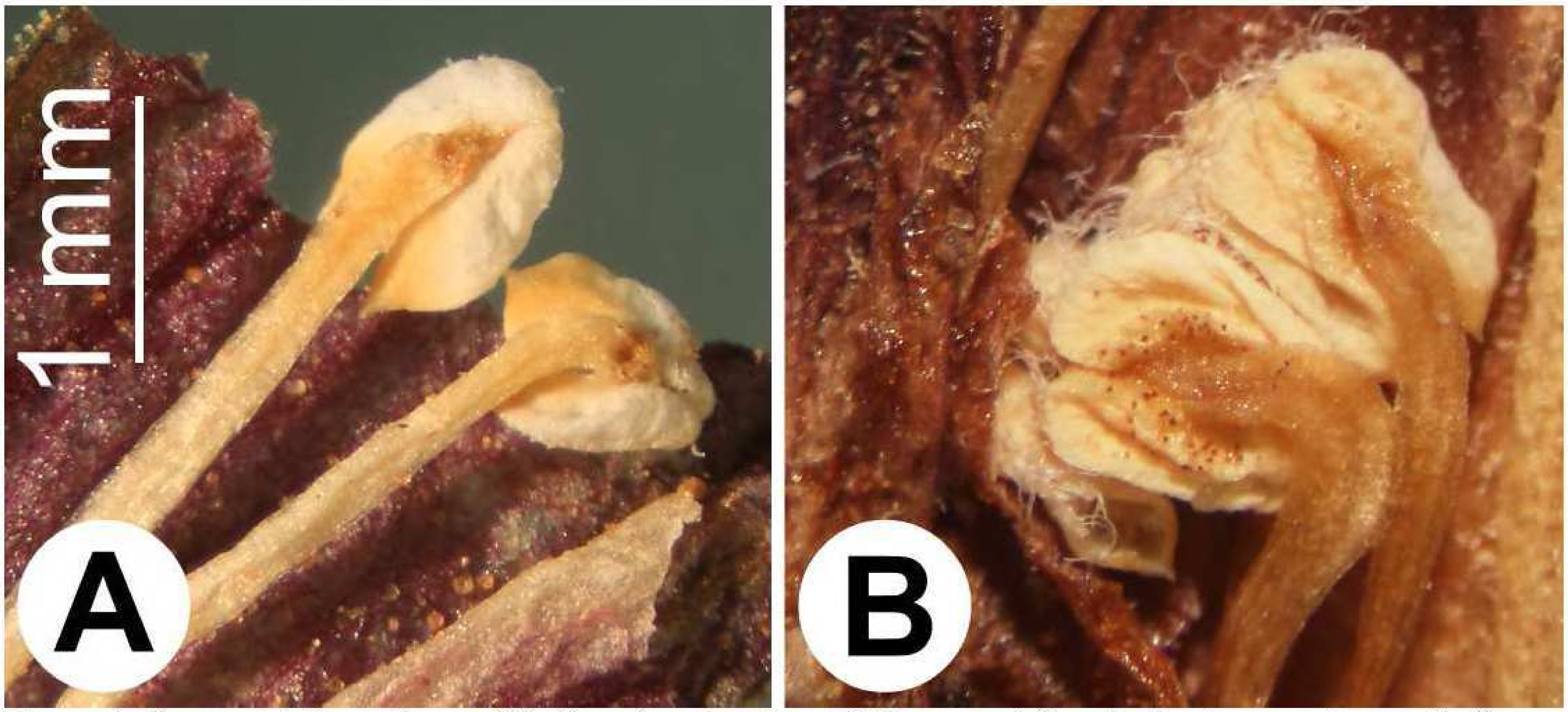

Figure 6. Representative anthers of *Orobanche arizonica* and *O. cooperi*, from herbarium specimens. A. *O. arizonica*, taken from *Holmgren & Hansen 3423* (NY); note glabrous anthers. B. *O. cooperi* subsp. *latiloba*, taken from *Shreve 10163* (ARIZ); note minute spherical glands.

CHARACTER	*O. ARIZONICA*	*O. DUGESII*	*O. COOPERI*
CALYX	8–12 mm	7–9 mm	7–12 mm
COROLLA	15–20 mm, Tube narrow, Pubescent	12–15(–17) mm, tube slightly expanded, Glabrous or glabrate	(12–)15–32 mm, tube slightly expanded, Pubescent
LIPS/LOBES	3–5 mm, erect	3 mm, erect	5–10 mm, reflexed, erect or revolute
COLOR	Purple tinted, corolla lobes purple, tube white	Yellowish with rose tint, thin membraneous	Dark purple, corolla dark purple w/white throat
UPPER LOBES `	Triangular acute, not apiculate	truncate, minute apiculate tooth	Triangular acute, distinct *apiculate tooth
PALATAL FOLDS	Pubescent	Glabrous	Pubescent
PUBESCENCE	Glandular pubescent	Glabrous or nearly so	Glandular pubescent
FLOWERING	June–August	May–June	December–April
HOST	*Gutierrrezia*	Unreported, possibly Asteraceae	*Ambrosia, Sidneya, Encelia*
DISTRIBUTION	Colorado Plateau, Southern Great Basin Desert	Trans-Mexican Volcanic Belt	Sonoran Desert , Chihuahuan Desert

Table 1. Comparative characters for three species of *Orobanche*. *Sometimes absent in *O. cooperi* subsp. *cooperi*.

CHARACTER	***O. DUGESII***	***O. COOPERI*** **SUBSP. *PALMERI***
CALYX	7–9 mm	8–12 mm
COROLLA	12–15 (17) mm,	15--18 mm,
LIPS/LOBES	3 mm, erect	4–6 mm, reflexed or revolute
COLOR	Yellowish, corolla with rose or purple tint, thin membranous	Dark purple, corolla dark purple w/white throat
UPPER LOBES `	Truncate or round, minute apiculate tooth	Triangular acute, apiculate tip
PALATAL FOLDS	Glabrous	Pubescent
STAMEN	Anthers glabrous, No dorsal glands	Anthers pubescent, dorsal glands
PUBESCENCE	Glabrous or nearly so	Glandular pubescent
FLOWERING	May–June, date absent on most specimens	December–April
HOST	Unreported, possibly Asteraceae	*Sidneya*

Table 2. Comparative characters of *Orobanche dugesii* and *Orobanche cooperi,* subsp. *palmeri.*

Relationships of *Orobanche multicaulis*

The question of the relationship of *Orobanche cooperi* to *O. multicaulis* must be resolved in order to clarify species circumscriptions in the *O. ludoviciana* complex. Questions have existed for some time regarding the morphological distinction between these two taxa. Although Felger (2000) placed *O. multicaulis* in synonymy with *O. cooperi,* most treatments have maintained the two binomials as separate species. It is well known among field botanists familiar with the Sonoran Desert flora that these two taxa share many morphological characters and ecological requirements and are difficult to distinguish. Both are largely confined to the Sonoran Desert (except *O. multicaulis* subsp. *palmeri* Munz) and utilize the following perennial hosts (all in the Asteraceae tribe Heliantheae): *Ambrosia dumosa* (A. Gray) W.W. Payne, *A. deltoidea* (Torr.) W.W. Payne, *A. salsola* (Torr. & A. Gray) Strother & B.G. Baldwin, as well as *Encelia farinosa* A. Gray ex Torr., and *Sidneya* (*Viguiera sensu lato*). Other hosts are occasionally reported but require confirmation.

The two species were treated by Collins (1973) in a manner that made it appear that *Orobanche cooperi* occurred only in Arizona and California and *O. multicaulis* only in Sonora and Baja, Mexico. The implication was that the two species were somehow restricted at the border between Mexico and the United States. There are no geographical or ecological barriers to produce such a distribution. The lack of data to support this peculiar distribution required a thorough reexamination of the two taxa for the preparation of the treatment for *Flora of North America.*

The original description of *Orobanche cooperi* was published by Gray (1885) under the binomial *Aphyllon cooperi.* Later, Heller (1898) transferred it to the genus *Orobanche.* Beck (1930) and Munz (1930) treated it as a variety of *O. ludoviciana.* Munz further recognized four varieties under the name *O. ludoviciana*: var. *"genuina"* (var. *ludoviciana*), var. *cooperi* (A. Gray) Beck, var. *latiloba* Munz, and var. *valida* (Jeps.) Munz. Shreve and Wiggins (1964) and Felger (2000) treated *O. cooperi* as a species but did not recognize varieties, placing *O. ludoviciana* var. *latiloba* in synonomy under *O. cooperi.* Many current botanists continue to treat these taxa as *O. ludoviciana* var. *cooperi* and var. *latiloba* following Munz (Kearney & Peebles 1960). However, the nomenclature for these infraspecific taxa as varieties or subspecies of *O. cooperi* has not been validly published. *Orobanche valida* Jeps. was established as a California endemic by Heckard and Collins (1982). *Orobanche ludoviciana* is now recognized as a prairie and glade species occurring mainly in the Great Plains of North America and some adjacent areas. Collins *et al.* (2009) presented a summary of the morphological characters of *O. cooperi* and *O. ludoviciana,* as well as their segregate, *O. riparia* L.T. Collins.

The original description for *Orobanche multicaulis* was published by Brandegee (1916). Later, Munz (1930) recognized two varieties, var. *"genuina"* (= var. *multicaulis*) in the Sonoran Desert and var. p*almeri* Munz in the Chihuahuan Desert. Collins (1971) treated var. *palmeri* in Texas as *O. cooperi.* There has since been no change in its taxonomic status. Although Munz (1930) recognized *O. multicaulis* and *O. cooperi* as separate entities, he cited only three specimens of *O. multicaulis* var. *"genuina,"* including the type, and only five specimens of var. *palmeri.* The limited material examined by Munz did not allow a complete assessment of the morphological variation and geographic range of the species. Collins (1973) examined approximately 30 herbarium exsiccate identified as *O. multicaulis.* He concluded that an apical tooth on the corolla lobes and stalked glands on the dorsal surface of the anthers could be used to separate it from *O. cooperi.* The presence of some intermediate specimens was noted, but the question of the relationship between *O. cooperi* and *O. multicaulis* was not resolved. Munz (1930) indicated the palatal folds were poorly developed in *O. multicaulis,* but that character does not hold up on close examination.

Over the last three decades, significant new collections have accumulated in various herbaria to augment the data from the earlier studies. For the present reassessment, 226 exsiccate of *Orobanche multicaulis* (var. *multicaulis*) and *O. cooperi* (var. *latiloba*) were examined. Specimens studied were from Arizona, California, Sonora, and Baja California. The nature of *Orobanche* is such that most of the morphological variation is in the inflorescence and flowers. The flowers were examined for typical characters of length, pubescence, nature of the lobes, and shape and vestiture of the stamens. This confirmed that there were no identifiable discontinuities between specimens identified as *O. cooperi* or *O. multicaulis.* Morphologically, the plants appear identical in size, color, floral anatomy, and pubescence. These observations indicate that, in addition to their overall similarity, the two taxa share the characters of stalked glands on the dorsal surface of the anthers (Fig. 3B) and an apical tooth on each of the upper corolla lobes. These features are present in specimens throughout the geographical range of the complex and are generally not present in other species of *Orobanche.* The absence of the apical tooth on corolla lobes and stalked glands on the anthers from some specimens of *O. cooperi* var. *cooperi* is an exception (see discussion below under *O. cooperi.*) Additionally, the two traditionally recognized taxa utilize the same hosts and occur in similar ecological situations. Because the two taxa share important morphological character states, we conclude that they should be combined under one binomial, *O. cooperi*, based on nomenclatural priority. The result is an expanded circumscription of *O. cooperi* that includes the former *O. multicaulis* var. *multicaulis* and var. *palmeri*. This new combination further supports the conclusion that *O. multicaulis* and *O. dugesii* are not conspecific.

TAXONOMY

The following key is presented to provide identification for species in the *Orobanche ludoviciana* complex in North America and differentiate this complex from the *O. californica* complex. Descriptions follow only for the species and subspecies for which nomenclatural changes have been made.

1. Inflorescence compact or open corymb or corymbose (some subspecies of *O. californica* appear short-racemose) .... **Orobanche californica** complex (for key, see Heckard 1973)
1. Inflorescences compact or open, simple or compound spike-like racemes .... **Orobanche ludoviciana** complex

  2. Corolla lobes rounded, (rarely deltate and bluntly pointed in *O. ludoviciana*).

    3. Corollas 14–20 mm, the tube pale or whitish externally, lips 3–6 mm, rose or dark purple, palatal folds pubescent, anthers glabrous or pubescent, inflorescence uniformly glandular pubescent, not appearing whitish canescent .... **Orobanche ludoviciana**
    3. Corollas 22–36 mm, the tube yellow or whitish externally, lips 5–12 mm, lavender, rose, or sometimes purple, anthers woolly, palatal folds densely pubescent, plants densely glandular pubescent, appearing whitish-canescent .... **Orobanche multiflora**

  2. Corolla lobes pointed, triangular, acute or truncate but then with or without apiculate tooth.

    4. Corollas pale yellow with rose- or purple-tinged lobes, glabrous or nearly so, lobes truncate, barely erect, with minutely apiculate tooth, anthers glabrous or nearly so, plants glabrous or nearly so .... **Orobanche dugesii**
    4. Corollas dark purple or lavender or the tube white with dark purple lobes, densely glandular pubescent, lobes pointed, triangular acute or obtuse, distinctly erect, reflexed or revolute, with or without apiculate tooth, anthers usually pubescent, plants densely glandular pubescent.

      5. Corollas (12–)16–32 mm, lips 4–10 mm, the lobes erect, reflexed or revolute, with an apiculate tooth, anthers with stalked glands on the dorsal surface (sometimes absent in subsp. *cooperi*) .... **Orobanche cooperi**
      5. Corollas 12–20 mm, lips 4–8 mm, lobes erect or slightly reflexed, lacking an apiculate tooth, anthers lacking stalked glands.

        6. Corollas 12–16 mm, dark purple, the distal portion of the tube and lip dark purple, white and purple striped proximally, the lobe tips dark purple; filaments pubescent at base; bracteoles equaling or exceeding the calyx; plants endemic to California; hosts *Garrya and Eriodictyon* .... **Orobanche valida**
        6. Corollas 15–22 mm, the tube pale white or lavender, the upper lip purple or lavender; filaments glabrous at base; bracteoles much shorter than calyx; plants not from California; hosts Asteraceae.

          7. Corollas 15–20 mm, the tube narrow, whitish, the lobes narrowly triangular, dark purple; plants of high desert in N Arizona and S Utah; hosts shrubby species of *Gutierrezia* .... **Orobanche arizonica**
          7. Corollas 15–22 mm, the tube slightly flared, lavender, or pallid white with dark purple veins, the upper lobes broadly triangular, purple or pale lavender; plants of riparian areas; hosts annual species of *Ambrosia* and *Xanthium* .... **Orobanche riparia**

Orobanche Ludoviciana Cooperi

Corolla 15-16 mm. long, lobes ca. 5 mm., triangular, acute but not abruptly acute, palatal folds prominent. The rather long (fully 9 mm.) and lanceolate calyx-lobes, and tendency of the caulin bracts to be acute rather than rounded, apparently are characters suggesting intergradation with var. genuina. (RHP, 1935)

floral pubescence/[illegible]

PLANTS OF ARIZONA

Orobanche Ludoviciana Cooperi (Gray) Beck

Corolla dull purple.

Marsh near Tuba City, Coconino County.
Elev. 5050 ft.

No. 12867 T. H. KEARNEY R. H. PEEBLES Collectors Sept. 27, 1935

HERBARIUM OF THE UNIVERSITY OF WISCONSIN
REVISION OF OROBANCHE SECT. MYZORRHIZA
OROBANCHE COOPERI (Gray) Heller
ssp. COOPERI

Turner Collins, 1972

HERBARIUM OF THE
U. S. FIELD STATION
SACATON, ARIZONA

Figure 7. Holotype of *Orobanche arizonica* (*Kearney & Peebles 12867* [US]).

Figure 8. Holotype of *Orobanche dugesii* (*Duges s.n.* [GH]); the inset in the upper left is from the righthand plant on the sheet.

1. **OROBANCHE COOPERI** (A. Gray) A. Heller, Cat. N. Amer. Pl., 7. 1898. *Aphyllon cooperi* A. Gray, Proc. Amer. Acad. 20: 397. 1885. *Orobanche ludoviciana* var. *cooperi* (A. Gray) Beck, Bibl. Bot. 4: 81. 1890. *Myzorrhiza cooperi* (A. Gray) Rydb., Bull. Torrey Bot. Club 36: 695. 1909. **TYPE: USA. Arizona**. Mojave Co.: Ft. Mojave, 1860, *Cooper s.n.* (lectotype [chosen inadvertently by Munz (1930, p. 621)]: GH!; isolectotypes: NY!, US!, K!). Cooper's broomrape, desert broomrape

Plants 5–45 cm, stems simple or branched, base often enlarged, glabrous below. **Roots** numerous, slender and branching, forming an amorphous mass around the infection. **Leaves** 5–13 mm, lanceolate to ovate, apex acute or obtuse. Inflorescences spike-like racemes, purple, copiously viscid-glandular pubescent, sometimes appearing canescent. **Inflorescences** usually dark purple, densely glandular viscid-pubescent. **Bracts** 5–12 mm, lanceolate, purple, apex acuminate, erect or reflexed, glandular puberulent. **Pedicels** proximal 10–30 mm, distal 0–5 mm, bracteoles 2. **Calyces** 7–12 mm, dark purple, deeply five cleft into lance acute-attenuate lobes, densely glandular pubescent. **Corollas** (12–)16–32 mm, the tube white, the lobes purple, constricted above ovary and bent forward, densely glandular-pubescent to glandular-puberulent externally, palatal folds prominent and densely pubescent; lower lip 4–7 mm, lobes extended or spreading or slightly reflexed, dark purple to pale lavender usually with three dark veins in each lobe, apex acute; upper lip 6–10 mm, shallowly cleft, dark purple, erect, reflexed, or revolute, the lobes broadly to narrowly triangular with or sometimes without apiculate tooth, densely pubescent with eglandular hairs. **Stamens**: filaments glabrous; anthers glabrous or tomentulose along the sutures, included, stalked glands on dorsal surface, sometimes absent. **Stigma** peltate, discoid-crateriform, bilaminar, or rhomboid, margins entire or crenulate. **Capsules** 6–12 mm, ovate. Seeds 0.2–0.5 mm, favose, tan to dark brown.. 2n = 48, 72, 96 (Raven et al. 1965; Collins 1973; Heckard & Chuang 1975).

Flowering Jan–May. 30–2000 m. Ariz., Calif., N Mex., Tex., Mexico (Baja California, Chihuahua, Coahuila, Durango, Hidalgo, Nuevo León, San Luis Potosí, Sonora.). Warm desert, sandy flats, washes, dunes, and mountains. Hosts: Asteraceae: Heliantheae (generally *Ambrosia, Encelia,* and *Sidneya* [*Viguiera* sensu lato]).

Orobanche cooperi is widely distributed primarily in the Sonoran, and Chihuahuan Deserts. The three entities treated here as comprising this species have been treated at various taxonomic ranks historically (see above). We treat them here as subspecies primarily for the sake of consistency, as this rank has been utilized in recent decades to denote infraspecific taxa in other North American members of the genus *Orobanche* (Heckard 1973; White & Holmes 2001).

From the available counts, it is clear that *Orobanche cooperi* comprises a polyploid complex. In discussing variations in ploidy among California populations, Heckard and Chuang (1975) advised caution in ascribing particular levels of ploidy to the infraspecific taxa known to them. They noted a tendency in California for $2n$=96 plants to have smaller, shorter-lobed corollas and peltate-bowl-shaped stigmas, compared with $2n$=48 plants, which they described as having somewhat larger corollas and peltate-crateriform, often bilobed stigmas. However, they were unable to observe the same morphological correlations with ploidy in plants from Baja California and did not study plants from elsewhere in the range of the species (Fig. 5). Heckard and Chuang further noted that plants with $2n$=72 are possibly hybrids resulting from hybridization in mixed populations. This situation cannot be resolved without additional research, and it is possible that other subspecies might be detected in the future. It should be noted that the only available count for subsp. *palmeri* is $2n$=48 (Collins 1973, as *O. multicaulis* var. *palmeri*).

Key to subspecies

1. Corollas 22–32 mm, lips 6–10 mm, upper lobes erect or reflexed, with an apiculate tooth: anthers pubescent, with stalked glands on dorsal surface; Sonoran Desert .... 1b. **Orobanche cooperi** subsp. **latiloba**

1. Corollas 15–22 mm, lips 4–9 mm, upper lobes erect, reflexed, or revolute, with or sometimes without an apiculate tooth; anthers sparingly villous or glabrous, stalked glands sometimes absent (2).

2. Corollas (15–)18–22 mm, lips 5–9 mm, upper lip erect or reflexed, the lobes triangular, with or without an apiculate tooth, anthers glabrous or sparingly villous, stalked glands present or sometimes absent; Sonoran Desert .... 1a. **Orobanche cooperi** subsp. **cooperi**

2. Corollas (12–)15–20 mm, lips 4–6 mm, lip reflexed or revolute, with or rarely without apiculate tooth; anthers variously pubescent or glabrous, stalked glands few or sometimes absent; stigma peltate or frequently bilaminar; Chihuahuan Desert .... 1c. **Orobanche cooperi** subsp. **palmeri**

1a. Orobanche cooperi subsp. **cooperi** (Fig. 5).

Stems simple or branched, sometimes enlarged proximally. **Bracts** 8–11(–13) mm, broadly to narrowly lanceolate, dark purple or pale, apex not or only slightly reflexed. **Calyces** 7–10 mm, dark purple or lavender. **Corollas** (15–)18–22 mm, lips 5–9 mm, purple or rarely yellow, upper lobes triangular with or without apiculate tooth, erect, palatal folds pubescent. **Anthers** glabrous or sparingly villous, stalked glands present or sometimes absent. **Stigmas** peltate, bilaminar, or rarely bilobed.

Flowering Jan–Apr. Ariz., Calif., Mex. (Sonora). 30–1000 m. Warm sandy desert and dry washes of the Sonoran Desert.

The range of this subspecies is primarily in Arizona (south of the Mogollon Rim) and southern California and extends into the extreme northern part of Sonora and Baja California. It is sympatric with subsp. *latiloba* throughout almost its entire range.

1b. Orobanche cooperi subsp. **latiloba** (Munz) L.T. Collins **comb. et stat. nov.** *Orobanche ludoviciana* Nutt. var. *latiloba* Munz, Bull Torr. Bot. Club 57: 621, 1931. **TYPE: USA. California**. Riverside Co.: Colorado Desert, 22 Apr 1922, *Munz & Keck 4960* (holotype: RSA!; isotype: US). Fig. 5.

Orobanche multicaulis Munz, Bull. Torrey Bot. Club 57: 613. 1931. **TYPE: Mexico. Baja California**. Purissima, 1889, *Brandegee s.n.* (holotype: C!) (Figs. 5, 7).

Stems simple or frequently branched, often enlarged proximally. **Leaves** 8–12 mm, broad lanceolate, apex obtuse, rarely imbricate proximally. **Bracts** 7–11 mm, broadly lanceolate, dark purple, apex acuminate or obtuse, slightly reflexed. **Calyces** 8–12 mm, dark purple or lavender, lobes sometimes reflexed. **Corollas** 22–32 mm, lips 6–10 mm, upper lobes with apiculate tooth, erect or reflexed, palatal folds densely villous. **Anthers** pubescent, stalked glands on dorsal surface. **Stigmas** peltate or frequently bilaminar, rhomboid.

Flowering Jan–Apr. 30–1000 m. Warm sandy desert and dry washes of Sonoran Desert. Ariz., Calif., Mex. (Baja California, Sonora)

The nomenclatural change to subsp. *latiloba* makes it the most widely distributed subspecies of *Orobanche cooperi*. Although Martin et al. (1998) noted it in the Rio Mayo region of southern Sonora, Mexico, we observed that some specimens examined from that area do not fit into the circumscription of *O. cooper* subsp. *latiloba* or any other recognized taxon of North American

Orobanche. It should further be noted that there are a few sheets from several states elsewhere in Mexico that are anomalous morphologically and require further study.

1c. **Orobanche cooperi** subsp. **palmeri** (Munz) L.T. Collins **comb. et stat. nov.** *Orobanche multicaulis* var. *palmeri* Munz, Bull. Torrey Bot. Club 57: 613. 1931. TYPE: **MEXICO. Durango**. Durango, 1896, *Palmer 7* (holotype: GH!; isotypes: F!, K!, NY!, US!) (Fig. 5).

Stems 5–30 cm, densely glandular viscid pubescent above, sometimes branched and enlarged below. **Leaves** 6–10 mm, narrowly lanceolate to broadly ovate, imbricate proximally. **Bracts** 7–12 mm, dark purple, narrowly lanceolate to linear, apex acute to acuminate, strongly reflexed, glandular pubescent. **Pedicels** 0–8(–15 proximally) mm. **Calyces** 8–12 mm, dark purple, lobes reflexed. **Corollas** 15–18(–22) mm, abaxial lobes 3–5 mm, reflexed, with 1–3 dark veins, upper lobes 4–6 mm, reflexed or revolute, with or sometimes without apiculate tooth, sometimes truncate, palatal folds densely villous distally. **Filaments** glabrous, anthers glabrous or tomentulose along suture, stalked glands few, often obscure. **Stigmas** bilaminar, rhomboid. **Capsules** 8–12 mm, narrowly ovate.

Flowering Jan–May. (500–)700–2000 m. N. Mex., Tex., Mex. (Chihuahua, Coahuila, Durango, Hidalgo, Nuevo León, San Louis Potosí). Volcanic mountains, sand dunes, dry washes in Chihuahuan Desert. Host: *Sidneya tenuifolia* (A. Gray) E.E. Schill. & Panero (*Viguiera stenoloba* S.F. Blake).

Subsp. *palmeri* is distributed entirely in the Chihuahuan Desert from western Texas and southern New Mexico southward into Mexico, in rocky ravines, dry washes, and on hillsides. It is allopatric with the other two subspecies of *Orobanche cooperi*. Its host association with *Sidneya* sets it apart from the Sonoran Desert subspecies that utilize mostly *Ambrosia*. However, there are relatively few reliable host reports for this taxon and it may parasitize additional perennial species of Asteraceae tribe Heliantheae.

The type collection of subsp. *palmeri* is aberrant in that the inflorescences and flowers are somewhat distorted. This likely occurred as a result of the developing inflorescences having to push up through densely rocky or otherwise highly compacted soil.

2. **Orobanche arizonica** L.T. Collins, **sp. nov.** TYPE: **USA. Arizona**. Coconino Co.: Near Tuba City, 5500 ft., *Kearney & Peebles 12867* (holotype: ARIZ!; isotype: US!) (Figs. 1, 2, 3A, 4, 5, 8). Arizona broomrape

Similar to *Orobanche cooperi* in its triangular and pointed corolla lobes, but differing in the apiculate lobe apex and glands absent from the anthers.

Plants 5–35 cm, solitary or clustered, rarely branched, stem base not enlarged, glabrous proximally. **Roots** few, short, inconspicuous. **Leaves** 4–10 mm, lanceolate to broadly ovate, glabrous. **Inflorescences** dense spike-like racemes, dark purple or sometimes pale lavender, viscid glandular-pubescent. **Bracts** 5–11 mm, narrowly oblong-lanceolate, apex acute, pubescent. **Pedicels** 0–5(–15 proximally) mm; bracteoles 2. **Calyces** 8–12(–14) mm, deeply 5-lobed, the lobes 6–7(–10) mm, lance-linear to linear-subulate, about equal in length, densely glandular pubescent. **Corollas** 15–20(–22) mm, the tube white, constricted above the ovary, exterior glandular puberulent or pubescent, palatal folds yellow, villous distally with eglandular trichomes; lower lip 3–4 mm, divided to its base into 3 linear lobes 1–2 mm wide, apex acute, pubescent with eglandular trichomes, often with 1–3 purple veins; upper lip ca. 4–6 mm, dark purple, erect, divided about half its length, the lobes triangular-acute or sometimes obtuse-rounded with denticulate margins, 2–3 mm wide, dark purple, densely pubescent with eglandular trichomes. **Stamens**: filaments glabrous or with a few scattered hairs; anthers glabrous or sparsely woolly from sutures of the thecae. **Stigmas** peltate, discoid-crateriform or rarely somewhat 2-parted. **Capsules** 6–10 mm. Seeds 0.3–0.5 mm, favose, tan to brown. 2n = 48 (Collins 1973).

Flowering June–Aug; pinyon-juniper woodlands, high desert, red sands; 1000–3000 m; Ariz., N. Mex., Utah.

The range of *Orobanche arizonica* is primarily north of the Mogollon Rim in Arizona, northward on the Colorado Plateau, and into the southern half of Utah and adjacent Colorado, but it extends sporadically southward in Arizona to the Chiricahua and Dragoon Mountains (Cochise County). It is often confused with *O. ludoviciana* or has been considered a small-flowered version of *O. cooperi*. It was treated most recently as *O. cooperi* by Heil et al. (2013). The two species can be distinguished on the basis of morphology, habitat, host associations, and phenology. It is parasitic on *Gutierrezia sarothrae* (Pursh) Britt. & Rusby (Asteraceae) and possibly other species of the genus.

Several specimens scattered through the range of *Orobanche arizonica* were exceptional in that they had corolla lobe characters that varied from the majority of specimens examined. These variations included corolla lobes that were somewhat rounded, truncate and denticulate, or lobes that were translucent in prepared specimens. The latter condition is common in *O. corymbosa*. Specific specimens cited with these condition are *Pilsbry s.n., Blakley 1319, Heil 13472, 13897, 17261*, and *Porter 1508*. The cause of this variation was not determined. However, given the proximity of other species raises the possibility of genetic exchange. Further, more detailed studies are needed within pertinent populations. The previously unpublished chromosome number from Collins (1973) is vouchered by two specimens from San Juan Co., Utah: *Collins 1538, 1539* (UWM). These were originally reported as *O. cooperi* subsp. *cooperi*, but the voucher determinations were reevaluated during the present project.

Specimens examined. **USA. Arizona**. Apache Co.: 10 mi N of Red Mesa Trading Post, 22 Aug 1952, *Deaver 4034* (ARIZ); Navajo Ind. Res. N end of Corrizo Mts., 3 Aug 1911, *Standley 1514* (US); Red sand dunes N of jct. Hwy 191 and 64, 4 Jun 2001, *O'Kane et al. 5213* (SJNM); Along White House Trail Canyon de Chelly Nat. Mon., 15 Jun 1973, *Dennis s.n.* (ARIZ); Active dunes N. side of Comb Ridge, ¼ mi. E of Navajo Co. line, 17 Aug 2001, *Heil & Clifford 17351* (SJNM); S end of Ventana Mesa, 3 mi W of Hwy 191, 4 mi N of Hwy 4, 27 May 1986, *Reeves 8286* (SJNM). Cochise Co.: 8 mi N of Portal 29 May 1952, *Blakley 1319* (DES); Buckeye Canyon, Chiracahua Mts., 3–30 Nov 1906, *Pilsbry s.n.* (PH); Cochise Stronghold, Dragoon Mts., 12–16 Oct 1910, *Pilsbry s.n.* (PH). Coconino Co.: Warm Springs Canyon, Kiabab Plateau, 30 Sept 1948, *Goodding 409-48* (ARIZ); Between Winslow and Flagstaff, 6 Jun 1935, *Peebles 12001* (ARIZ); 5 mi S of Tuba City, 8 Jun 1937, *Peebles 13362* (ARIZ); S of Navajo Mountain and Tin Can Canyon, 16, Aug 2001, *Heil & Clifford* 17261 (SJNM). Graham Co.: 12 mi NW of Duncan, 3 May 1973, *Holmgren 7066* (RSA). Navajo Co.: between Winslow and Holbrook, 21 May 1934, *McKelvey 4559* (A); Little Captain Valley along Comb Ridge, 16 Sept 2001, *Heil et al. 18064A* (SJNM); 1.5 mi NW from jct to Chilchinbito on Hwy 59, 24 Aug 2001, *Heil & Mietty 17622* (SJNM); Between Kayenta & Betatakin, 12 Sept 1938, *Eastwood & Howell 6571* (CAS); 5 mi NE of Holbrook, 18 Jun 1901, *Ward s.n.* (US); 13 mi S of Holbrook on Hwy 77, 24 Jun 1951, *Turner 2671* (WS); 8 mi N of Winslow, 22 May 1945, *Goodding 29-45* (ARIZ); Warm Springs Canyon below Ryan, 30 Sept 1948, *Goodding 409-48* (ARIZ). **Colorado**. Mesa Co.: Colodaro National Monument, mouth of Ute Canyon, 31 May 1982, *Weber, Wittman & Rector 16119* (COLO). **New Mexico**. Grant Co.: Red Rock CCC Camp, on *Gutierrezia*, 16 May 1935, *Maguire 11408* (NY). Rio Arriba Co.: BLM Rd 370, 5 mi E of Hwy 537, 28 Aug 1999, *Heil 13897* (SJNM). San Juan Co.: N of Waterlow in sand, 28 Jun 1984, *Porter 84*-420 (SJNM); Bisti Badlands, Di Na Zin Wilderness, 12 Aug 1986, *Porter 1508* (SJNM); San Juan floodplain, ½ mi NW of Head Canyon, 2 Jul 1999, *Heil 13472* (SJNM). **Utah**. Emery Co.: Capitol Reef Park, ½ mi N of Middle Desert Wash, 7 Jun 1986, *Heil 2547* (SJNM); Farnham, 29 Jun 1898, *Jones s.n.* (RSA). Garfield Co.: 2 mi NW of Four Mile Bench, 13 May 1987, *Heil 3107* (SJNM);

Dixie National Forest, 8 mi N of Escaliente, 11 Aug 1965, *Holmgren et al. 2420* (NY). San Juan Co.: Copper Canyon, 16 mi NW of Oljeto Post, 18 Jun 1938, *Cutler 2268* (MO); San Juan Canyon, 1 mi from Mexican Hat, 20 Jun 1938, *Cutler 2308* ((MO, NY); Copper Canyon Badlands, 11 Jun 1995, *Holmes 403* (SJNM); Monument Valley, 22 Jun 1944, *Holmgren 3423* (US); Rainbow Bridge National Monument, 7 Jun 1961, *Mason & Phillips 1932* (ARIZ); 10 mi S of Montezuma Creek, 29 May 1984, *Porter 84-273* (SJNM). Washington Co.: St. George, 1874, *Parry s.n.* (MO); 5 mi NE of Kolob Arch, Timber Creek Trail, 18 Aug 1987, *Thorn & Franklin 5641* (SJNM). Wayne Co.: Capitol Reef Park, 0.5 mi N of confluence of Polk and Deep Creek, 3 Jun 1993, *Heil & Schles 7539* (SJNM); Capitol Reef Park, N entrance, Hwy 24, 25 Jun 1987, *Porter 5086* (SJNM).

3. **Orobanche dugesii** (S. Wats.) Munz, Bull. Torr. Bot. Club 37: 613. 1931. *Aphyllon dugesii* S. Wats., Proc. Amer. Acad. 18:132. 1883. **TYPE: MEXICO. Guanajuato**. 1880, *Duges s.n.* (holotype GH!). (Figs. 5, 6). Duges' broomrape

Plants 5–12(–23) cm, stems simple or occasionally branched above, glabrate, pallid-yellow, tan, rose- or purple-tinged. **Roots** usually few, short, sometimes in a globose mass, 10 mm or less. **Leaves** 5–10(–13) mm, lanceolate to ovate, apex obtuse, glabrous or with ciliate margins. **Inflorescences** spike-like racemes, glabrous or nearly so. **Bracts** 6–9 mm, lanceolate, apex acuminate, mostly appressed, yellowish or purple. **Pedicels** 0–4 (proximal –15) mm; bracteoles 2. **Calyces** 7–9 mm, yellowish or purple, deeply 5-cleft into lance acute-attenuate lobes. **Corollas** 12–17 mm, pale yellow tinted with purple, tube constricted above ovary and only slightly bent, glabrous, or glabrate, palatal folds glabrous; abaxial lip 3 mm, lobes extended, pale yellowish or rose tinged, apex truncate with minute tooth; adaxial lip 3–4 mm, shallowly cleft, yellowish, rose tinged or purple, slightly erect, the lobes obtuse or truncate with apiculate tooth, glabrous or nearly so. **Stamens**: filaments glabrous; anthers glabrous, included. **Stigmas** peltate, discoid-crateriform, or bilobed. **Capsules** 7–9 mm, ovate. **Seeds** 0.2–0.5 mm, favose, dark brown.

Flowering Jan–May. 2000–2500 m. Mexico (Guanajuato, Jalisco, Michoacán, Oaxaca, Puebla).

The geographic distribution of *Orobanche dugesii* seems to be associated mainly with the Trans-Mexican Volcanic Belt of central Mexico (Clausen 1959). Host data are unreported on most specimens. A report of "buffalo grass" as a host is questionable, as there are no valid reports of grasses or monocots as host plants for *Orobanche* sect. *Nothaphyllon.*

Of the several specimens examined, most were collected between 1880 and 1910. The most recent collections were one each from 1938 and 1940. The incomplete data on ecology, geographic distribution, and hosts results in an incomplete presentation of *Orobanche dugesii.* Thus no formal taxonomic revision is presented here.

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